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Division of Mycology and Disease Survey

BUREAU OF PLANT INDUSTRY, SOILS, AND AGRICULTURAL ENGINEERING

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INSECT-TRANSMITTED PLANT DISEASES: A SYMPOSIUM

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THE PLANT DISEASE SURVEY
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INSECT-TRANSMITTED PLANT DISEASES: A SYMPOSIUM

Joint Symposium on Insect-Transmitted Plant Diseases of the American Phytopathological Society, the American Association of Economic Entomologists and the Entomological Society of America.

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The part insects play in the transmission of plant diseases is a field of biology of rapidly increasing interest to the entomologist, the plant pathologist, and the plant breeder. With each passing season we add some new information to our total knowledge of the problem and achieve a better understanding of the significance of viruses in the agricultural economy of the country.

The role of insects in the transmission of plant diseases was a long neglected field of research. It lay in a so-called "no man's land" between two important branches of biology. From the standpoint of successful control of a destructive disease, there is perhaps no phase of plant pathology more fundamentally important than that dealing with the methods by which the disease is spread from plant to plant, field to field, and from one area to another. Yet few plant pathologists have devoted any great amount of effort to the study of insects in relation to the spread and development of plant diseases. The problem has been neglected to an equal degree by entomologists who, with few exceptions, have devoted their time and effort to insects causing direct injury to plants. Only recently has the more complex and obscure role of insects acting as vectors of plant diseases been given anything like the attention it deserves. This is becoming increasingly evident as we understand more fully the importance of viruses in our overall plant protection effort.

Phytopathologists and economic entomologists have one all-important interest in common -- the problem of plant protection. Workers in both fields are concerned with the protection of our agriculture from the innumerable pests which collectively take an enormous annual toll of our national production. Although this common interest exists, the two sciences have rather widely diverse interests, which may be explained to some degree by the origin of the two branches of biology. Not so many years ago, the broad field of biology was considered a highly specialized subject. It was considered possible for one man to obtain a fair mastery of available knowledge in the field. However, with the passing of time, knowledge in the field increased so rapidly that most investigators have come more and more to specialization. First, biology was divided into botany and zoology. Later, each of these was divided and sub-divided, each segment developing more or less its own techniques and vocabularies. The purpose of my few remarks is to develop the thought that there is a vast area in which the botanical and zoological sciences are inseparable.

Nearly 60 years ago, Waite pioneered in the field of plant disease transmission by insects, showing that certain species were definitely of importance as vectors. He demonstrated that fire blight of pears could be transmitted by bees and wasps. As early as 1884, Forbes had expressed the opinion that fire blight (Erwinia amylovora) was transmitted from tree to tree by the tarnished plant bug. Some years later, his theory was verified by Stewart. In the thirty years that followed Petri's work with the olive fly and the bacterial olive-knot disease (Pseudomonas savastanoi), and E. F. Smith's demonstration that cucurbit bacterial wilt (Erwinia tracheiphila) was transmitted by the striped cucumber beetle, an increasing amount of interest was shown in the subject.

In 1920, Rand and Pierce summarized for publication existing knowledge of insect transmission of plant and animal diseases. The authors coordinated the literature in both fields. They recognized certain principles common to both. These broad principles were used as a basis for a practical classification of the known phenomena of insect transmission.

Owing, in part at least, to the interest created by this paper, the American Phytopathological Society and the American Association of Economic Entomologists held a joint symposium on "Insects as disseminators of plant diseases," at their annual meeting in Toronto in 1921.

The part played by insects in the transmission of fungus disease likewise began to receive more attention. In 1847 Leunis had suggested the possibility that ergot (Claviceps purpurea) spores were spread by insects. Sturgis in 1898 suspected that insects were responsible for the transmission of the downy mildew (Phytophthora phaseoli) of lima beans. More recently, we have had such examples as chestnut blight (Endothia parasitica) and the Dutch Elm disease (Ceratostomella ulmi). The former depended on insects only to a limited degree. The latter, of course, is dependent to a large degree, if not entirely, on the activity of certain bark beetles. Of equal interest is the part that Ips play in spreading the fungus (Ceratostomella spp.) causing blue stain of conifers; and the relationship the wooly aphis has to the spread of perennial canker (Neofabraea perennans) and European canker (Nectria galligena) of apples.

The spread of virus diseases is more closely associated with insects than any other group of plant pathogens. Most true virus diseases of plants appear to be, at least to some extent, transmitted by insects -- and there are a number that are transmitted in nature only by insects. During

the past 35 years many virus diseases have been described and new ones continue to be reported with alarming frequency. As we delve deeper into this complex phase of biology, we find one or more viruses associated with nearly every cultivated crop. Some are subject to attack by many different viruses as in the case of potatoes. Certain others, such as curly top of sugar beets, aster yellows, and spotted wilt of tomatoes, have a wide host range among both weeds and cultivated plants. Since Takami in Japan in 1901 reached the conclusion that the dwarf disease of rice was caused by the feeding of the leaf hopper (Nephotettix apicalis) much has been learned in this important field. Today there are at least 125 viruses known to be insect transmitted. It is difficult to forecast the future. However, sufficient progress has been made to suggest that viruses constitute the biological challenge of this century.

To add complications to an already complex problem, it has been found that the transmission of viruses through seed occurs in some instances. This has been demonstrated with the common bean and certain other legumes, wild cucumber, muskmelon, potato, lettuce, and tomato. Hildebrand in 1945 and Cochran in 1946 announced evidence that viruses were transmitted through cherry seeds. About the same time pollen was incriminated. Then came Fukushi's work demonstrating that a virus could be transmitted congenitally from one insect generation to the next through the egg. Working with Nephotettix apicalis, he succeeded in demonstrating congenital transmission for seven successive generations.

Two important factors are fundamental to the control of an insect-borne virus disease of plants. It is essential first to determine the vector or vectors responsible for transmission. This has proved simple in the case of some diseases, but extremely difficult in others. To fully appreciate the complexity of the problem, we need only recall the years of work that have been devoted to the study of aster yellows, peach yellows, phloem necrosis of elm, phony peach disease, tristeza disease of citrus, and the quick decline of citrus. Moreover, once the mode of transmission is determined, we have reached only the half-way mark in solving the problem. An economic and practical means of destroying the vector must be found. This frequently introduces such problems as plant tolerances, and plant and soil residues, both of which are attracting the interest of the Food and Drug Administration -- and even committees of Congress. Also, plaguing the research worker is the realization that, over a period of time, insects may develop races resistant to chemical controls now widely accepted as effective. Confronting the entomologists and plant pathologists is the degree to which some present-day chemicals are shotgun killers. They do not distinguish between friend and foe. For example, it is not uncommon for spider mites to become a problem following the use of DDT. Also certain species of aphids may increase rapidly following destruction of their parasites by some of the newer insecticides now in common use. Mites may present no particular problem except the damage they themselves do. However, many aphids are commonly recognized as associated with the spread of viruses and the damage they do directly may be incidental to the role they play in the transmission of disease.

To supplement modern methods of cultural, biological, and chemical control, we are coming more and more to recognize the important place that quarantines fill in preventing or delaying the spread of plant diseases and their insect vectors from one locality to another. Over the years, quarantine procedures have been developed which are highly effective in preventing the introduction into this country of both plant diseases and insects. A new virus disease may be of little concern unless a vector is present to spread it. Many insects that have proved efficient vectors of disease may cause little damage by direct feeding. Viruses present a very complex problem in the enforcement of quarantine, as it is not uncommon for symptoms to be masked to the extent that they cannot be detected by inspections. A virus of little consequence in a foreign country may find host material to its liking when introduced into this country. Likewise, a virus indigenous in wild host plants in the United States may prove of little concern except in the presence of an efficient vector.

Agriculture is becoming more and more a highly technical enterprise, and specialization in the many branches of biology must continue. However, somehow, in our overall plant protection effort, there must be closer integration of the efforts of the plant pathologist, the entomologist, the nematologist, the chemist who deals with fungicides, insecticides, and nemacides, and the engineer whose task it is to develop the specialized equipment so essential in efficient pest control.

It seems to me that plant protection warrants greater emphasis in our overall agricultural planning. To reduce losses caused by crop pests certainly is a logical way to increase production without adding acreage or seriously affecting the amount of manpower and equipment devoted to agricultural pursuits.

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GEOGRAPHICAL ISOLATION OF SOME VIRAL DISEASES

Francis O. Holmes

Some viral diseases are known to have essentially world-wide distribution. In general, this does not imply that they originated in more than one continent or that they reached other continental areas without the assistance of man. It seems entirely unnecessary to assume either of these explanations. These viruses, in most cases, are known to be carried by man from one continent to another in connection with the ordinary procedures of commerce.

Other viral diseases seem to have remained highly localized. Often these have evolved in association with one or a few host plants and one or a few closely allied arthropod vectors. Peach-yellows virus is a good example of this. It has been found only in the peach and in closely related rosaceous plants. A single leafhopper species is known as its vector. Although peaches are grown widely in temperate climates throughout the world, peach-yellows virus is known only in North America, and even there has not been found on the Pacific Coast, where the peach-canning industry is important. No fact in virology has been more surely established than this: a virus such as that which causes peach yellows arises only from an antecedent virus of the same type. No matter how many peach trees are grown in other countries, or in other parts of the United States, our present experience indicates that peach-yellows virus will occur in them only when circumstances permit its transfer from infected host plants in the eastern United States, to which it is now confined. Viruses do not arise de novo (that is, by spontaneous generation) any more than do higher animals or higher plants. The possibility of spontaneous generation remains for both viruses and higher organisms; its demonstration, to date, has failed.

An example of reciprocal cases of localization of viruses may be cited in connection with the sugar-beet industry. The sugar beets of North America have suffered from the attacks of sugar-beet curly-top virus for many years, but this virus is unknown in Europe. On the other hand, the sugar beets of Europe have suffered from the attacks of sugar-beet yellows virus, yet this virus, at least until recently (3), has been unknown in North America.

We may ask why some of the best known viruses are to be found on all continents. The answer is two-fold. These viruses are well known in part because they have been available for study in so many countries and in part because the very characteristics that have permitted their spread from one continent to another have also facilitated research. Cucumber-mosaic virus has an essentially world-wide distribution, apparently because it is transmitted in propagating material, including Easter lily bulbs and gladiolus corms. In the trade between nations, such propagating material has been widely distributed. Spotted-wilt virus, in like manner, has been sent from one continent to another in dahlia corms. Tobacco-mosaic virus has the distinction of not requiring living plant tissues for its importation into remote regions. It survives in dried tobacco tissues and enters new host plants in distant lands through contaminative contacts. Bean-mosaic virus and lettuce-mosaic virus are sent from one part of the world to another in seeds, some of which on germination give rise to infected seedlings from which transmissions to healthy neighboring seedlings can occur locally. It is not surprising that viruses such as these have reached all continents.

We may assume that we have already in this country most of the viruses that can be transported in dormant bulbs, corms, dried seeds, or dried leaves, insofar as these materials enter into commerce. It is probable, however, that some seed and bulb-transmitted viruses are still associated only with commercially unimportant plant species in their native lands.

DANGER OF INTRODUCING PATHOGENS

The permutations of agriculture may eventually bring an opportunity for the now-localized viruses to be transferred from their present hosts to some commercially more important, or more frequently and distantly transported, plants; in the seeds, corms, or leaves of these, they may then be transported to new areas. This seems to have happened recently in the case of tobacco-ringspot virus, long known in North America but only recently reported as occurring in Europe. Tobacco-ringspot virus does not remain viable in dried leaves or stems of infected tobacco plants long enough to spread to other continents in dried products made from tobacco or tobacco wastes. There has been some difference of opinion about its possible ability to remain viable in, and to pass through the seeds of, infected tobacco plants. Henderson and Wingard (5) failed to detect transmission through seeds in the case of 64,500 seedlings that they examined. Valleau (19) reported seed transmission, but did not state how frequently it occurred. It is well established, however, that this virus is capable of passing through nearly 20 percent of the seeds from infected

petunias (4). Recently the virus was reported by Köhler (11) as causing a disease of potatoes in Europe. It is thought that petunia seeds, or possibly tobacco seeds, may have carried this virus to Europe, and that the virus may have become established there in perennial hosts. Obviously, many other viruses that are now highly localized may subsequently move from continent to continent in a similar way in seeds or in other commercially important plant products. The oceanic barrier, of course, is permeable in both directions. Circumstances that finally permitted tobacco-ringspot virus to be transported to, and established in, the continent of Europe are paired with others that will eventually bring to North America certain viruses that are not yet known here.

Experience has shown that the time required to devise control measures after a disease has spread to a new area may allow very great losses in current crops. When sugar-cane mosaic virus began to affect cane crops in the West Indies and the Hawaiian Islands, active investigations were begun to devise means of controlling the induced disease. These investigations eventually were successful and the disease was controlled by the use of resistant varieties, though severe losses were sustained while the investigations were in progress. In more recent years, the effort to produce resistant varieties of sugar beet to use in areas affected by sugar-beet curly top was also crowned by success, but the necessary research was carried on in the face of severe current losses. In a few cases, to be sure, considerable foresight has been used. Fiji disease of sugar cane has not reached the Hawaiian Islands as yet, but its vector is there and the disease might become very damaging if introduced, especially if an additional vector or additional vectors should be met to increase the rate of spread. Some efforts have been made to prepare for such an eventuality. The attempt at preparation of adequate control measures in advance by studies carried on where the disease exists already, is likely to prove a more economical though less spectacular procedure than an attempt to devise measures for control in the face of an outbreak of disease.

Some viral diseases have been studied enough to show that all commonly cultivated varieties of their host plants are susceptible to infection. This is true, for example, of peach-yellows, which is thought to be capable of infecting all available varieties of the peach. It is true also for peanut rosette, which has greatly interfered with the cultivation of peanuts in Africa, an essential part of the effort to increase the supply of edible oils for the British Empire. All varieties of peanut seem to have proved about equally susceptible. A third viral disease shares this superficially discouraging outlook. Sugar-beet yellows has caused extensive losses in field and garden beets of Europe and the British Isles. No variety of the host plant has proved usefully resistant.

It would be unwise to assume, however, that efforts to produce useful resistance in these three cases or others of the same sort would be destined to certain failure. The problem would be equally serious for potato-mottle infections were it not already known that a variety of potato can be completely immune to infection by this disease. All varieties of the potato once seemed susceptible. With the advent of the U. S. Department of Agriculture's seedling 41956 it became clear that the situation was not hopeless (17). This potato transmits its apparently complete immunity to hybrid progeny in such a way as to show that it possesses two dominant genes, both required for the immunity (18). This case is of special interest because single dominant genes for resistance are known in a number of cases, for example, in connection with resistances to tobacco mosaic in tobacco (6) and to spotted wilt in tomato (9, 7). In no such case, however, has anything approaching complete immunity been achieved. The possibility remains that the incorporation of two dominant genes conferring different types of resistance to a viral disease might lead to complete immunity in other species, as in the potato.

Until much more is known with respect to peach yellows, peanut rosette, and sugar-beet yellows, it seems unnecessary to regard these as hopeless cases. Indeed, their importance to the world at large suggests that they should be attacked vigorously, with the full expectation that measures for their control will emerge eventually and that information gained from studies on these viruses will prove useful in later attacks on related problems.

It would serve no useful purpose to attempt to list all of the viral diseases of plants that have remained to the present time in continents other than North America and that might cause serious losses to our crops if introduced. No one can prove that particular viruses would become established here if they should be imported once or repeatedly. The chance that they would do so lies for the most part in the province of those specifically dealing with biological warfare, and the arguments for and against survival of such viruses are, on this account, outside the province of the present paper.

It is, however, no secret that our corn crop is still free from viral diseases in the principal corn-producing area of the United States, that is to say, in the so-called Corn Belt. Warnings of the danger to our leading crop have been published already, so that our own agriculturists and those of other nations have been apprised of the situation (14, 13). In several parts of the world there are

diseases of corn that might cause our leading crop to be greatly damaged. One of these is the so-called maize stripe disease, the leafhopper vector of which occurs in the United States already. Maize stripe is a disease that stunts infected plants severely and prevents the development of grain on each plant that becomes infected before it has produced tassels (12). On the chance that it could become established if introduced, this disease might well be studied intensively in areas where it now exists, with a view to developing adequate means of control. The control measures would be immediately useful where the disease exists at present and would become of tremendous monetary value if the disease should appear later in areas of intensive corn production in this country.

Similarly our cotton crop suffers from no viral disease at present. In Africa, however, a serious viral disease of cotton, known as cotton leaf curl, is spread by the white fly, Bemisia gossypiperda (10). This and other viral diseases of cotton might well be studied where they now occur, to devise means of control, as insurance against extensive losses if they should become established in North America.

Our wheat crop is affected by a number of viral diseases, of which none have proved exceedingly important to date. Of our present wheat diseases, none is known to be transmitted by leafhoppers. The so-called winter-wheat mosaic, reported as being transmitted by the leafhopper Deltocephalus striatus L. in Russia, would seem to justify study in its present habitat, if that should be feasible, so that appropriate control measures would be available if it should reach here.

Our sugar-beet crop now has the advantage of resistance to curly-top disease as a result of prolonged studies of the Department of Agriculture, carried on for the most part in the presence of destruction caused by this disease. An unrelated but similarly destructive disease, the so-called sugar-beet yellows, occurs in Europe. Development of resistant varieties for this disease may require many years, for no source of resistance is now known, as has been stated. The cost of investigations to determine the feasibility of disease resistance for yellows would be exceedingly small now in comparison with losses that might be experienced if this disease should become established in the United States before adequate control measures become available. It may be mentioned that one of the principal arthropod vectors of this disease, the green peach aphid, Myzus persicae (Sulz.), is a common insect in this country.

NEW METHODS FOR CONTROL NEEDED

In an attempt to adapt known control measures to diseases not yet found in this continent, an opportunity may arise to develop new methods that will apply equally well to diseases already recognized here. Existing methods of control need to be supplemented. Each one succeeds better with some diseases than with others, because each has its limitations. Thus, roguing succeeds best with diseases that spread most slowly, and may fail entirely with diseases that spread very rapidly. Use of resistant varieties offers great economy in control for specific diseases for which it is available, but for some viral diseases such as peach yellows, sugar-beet yellows and peanut rosette, as has been indicated, no resistant varieties have been discovered to date. In some cases control of insect vectors proves effective but in others the vectors move so far, so constantly, or so frequently and infect plants in so short a time after settling on them that little or no control can be obtained by efforts directed against the vector insects. In potato diseases, isolation of plantings has been profitable, especially for production of seed stocks; isolation is more difficult to achieve with some other crops, however. For tomato spotted wilt and the cucumber-mosaic disease known as southern celery mosaic, destruction of weed reservoirs has been effective. In some diseases, choice of season for planting the crop may be a help. For other viral diseases, such as Pierce's disease of grape (22), all existing methods seem inadequate.

Many investigators are trying to devise new means of control for viral diseases. Much effort has been expended to learn how to control these diseases by chemotherapeutic measures. All claims for success in this field stand in need of confirmation. In the future, the chemotheropeutic approach will have an opportunity to prove what it can do. Recently it has been proposed that studies of ecology might permit the suppression of weed reservoirs by re-establishment of natural vegetation in areas where agricultural practices have disturbed normal successions of vegetation (15). This method may prove a valuable addition to our present means of control. Still other new means are urgently needed.

The threat of importation of viruses with their insect vectors, or of viruses that may find suitable vectors already in this country, cannot be completely eliminated by restrictions on importation of plant materials. We must assume that new diseases will enter the country from time to time. Quarantines on specific plant products help principally by reducing the rate of occurrence

of such introductions. It will not be possible to foresee with certainty which viruses will enter and become established nor the order in which they will appear. Naturally, therefore, it will not be possible to provide control measures in advance for all the diseases that may enter this country in the near future. At least some, however, of the potential introductions probably can be predicted. Study of these diseases in the areas in which they are now established, outside of this country, will be cheap insurance against future losses. An excellent example of this was provided recently by the study of South American curly top of beets by Dr. Bennett and his associates, whose published work has indicated that the introduction of this disease into North America would find us well prepared because of the resistance offered to this disease by varieties of sugar beet recently produced to control North American curly top (1). Again, spotted wilt of tomato, which has not yet proved important in the eastern United States, though it has been found there in small outbreaks for many years, has been studied in advance. An effective resistance for the strains that already occur in this area has been identified, used on a small scale (7), and preserved. If the virus should find a new reservoir plant in which it could build up to a high level, disastrous outbreaks might occur. The remedy, it is hoped, is at hand. If a remedy were not at hand, a few years of delay in developing resistance for such a disease might result in losses greatly exceeding the cost of the research necessary to provide means of control.

LOSSES FROM INCONSPICUOUS DISEASES

The extent of losses caused by diseases of moderate intensity often escapes notice. Much less important diseases, conspicuously involving a few plants and producing relatively unimportant destruction, may receive considerable publicity. The outright death of part of the plants in a crop or the death of tissues in the part of the plant that is commonly sold attracts the attention of growers and sometimes is noted also by the public. Diseases that do not prevent the sale of agricultural products but only lower their quality or slightly reduce yields may cause greater total losses without being much noticed.

Tobacco-mosaic disease has generally been regarded as of small importance. Losses have been estimated on many occasions to be of the order of 2 or 3 percent. Studies of quantity and quality of diseased plants, however, have brought evidence that estimates of loss generally have been much too low (20) and have given confidence that they are, in any case, not too high to represent the real losses. Assuming the conservative figure of 2 percent, the annual loss from this one disease in this country has been of the order of magnitude of twenty million dollars annually in tobacco alone. It may well be several times this amount, for even infection late in the season, as at topping time, when it no longer reduces yield in terms of weight, has been said to reduce yield in terms of dollars per acre very seriously, especially in dark tobacco varieties (8), by changes in grade of affected leaves when cured. Additional losses occur as a result of this disease in tomato and pepper. Because of the uniformity of its occurrence and the inconspicuous nature of the damage caused by this disease, the substantial total loss has hardly been noticed and it is only with the advent of rather satisfactory resistant varieties of tobacco in Kentucky and Virginia and with the current preparation of similar varieties for use in many of the other tobacco-growing States that the total losses of the past have begun to be more fully appreciated.

Other very inconspicuous viral diseases are similarly important. Almost every widely grown potato variety in the United States is carrying in every tuber, and so in every individual plant, the so-called potato-mottle virus (sometimes called potato-X virus). A number of strains of this virus are recognized and the effects of some are much more severe than those of others. In the absence of concurrent infection by other viruses, however, all strains are carried in most potato varieties without causing obvious disease. The mildest strains have proved difficult to detect even by transfer to standard test plants, such as Datura stramonium L. and Nicotiana glutinosa L., which mottle when infected by the commoner strains. Recently introduced test plants, such as Gomphrena globosa L. (21), are more widely applicable than those previously used, and serological tests were shown by Chester (2) to detect the mildest strains of this virus that are now known to exist. Losses attributable to the presence of strains of potato-mottle virus have been variously estimated. In a few cases no decrease of yield has been demonstrated, but in most cases losses seem to have been of the order of 9 to 22 percent (16). In view of the importance of the potato crop, the losses from infection by potato-mottle virus may be viewed as definitely detrimental to our productivity as a nation and, hence, to our standard of living. This loss accrues from the presence of a virus so apparently harmless as once to have been called the "healthy potato virus", that is, the virus of "healthy" potatoes. Unfortunately all varieties of potato that are now grown commercially are susceptible, although genetically immune varieties are in prospect. Incorporation of genetic immunity in commercially useful varieties of potato promises to

eliminate not only the losses now attributable to infection by potato-mottle virus alone, but also part of the losses attributable to infections by pairs of viruses of which potato-mottle virus is one of the destructive partners.

It is difficult to know which viruses cause the greatest damage to crops of the United States at the present time. It may well be, however, that the three most damaging viruses here at present are, first, potato-mottle virus, second, tobacco-mosaic virus, and third, cucumber-mosaic virus, if the criterion of total loss due to reduction in crop values, rather than losses in crop weights or volumes, is taken. If these are actually the three most important viruses affecting our plant-growing industries, it is interesting to note that no one of them alarms the farmer except in exceptional circumstances. Like hidden taxes, these viruses substract from income without being detected even by the farmers who suffer the losses directly, and naturally without being noticed by the public, whose standard of living is fractionally affected adversely. A fourth virus may belong with these three, and may even be found to precede the others when the truth is better known. This is alfalfa-mosaic virus, hardly perceptible in its effects on alfalfa, from which it was first isolated and which gave the virus its common name, but more obviously affecting such legumes as Ladino clover and a variety of other cultivated plants, including pepper and potato. Losses are extremely difficult to estimate in plants included in the hay crop of this country, which is no small item in our agriculture, however. The hay crop has a total valuation of some two and a quarter billion dollars a year, falling behind none of our crops except corn and cotton in 1950. In so fundamentally important a crop, even moderate losses, in constituent plants such as the clovers, may represent enormous total losses. These four well-known but little feared viruses deserve all the attention they have been given and more. Each individually costs our country more each year, in all probability, than all the research on viruses done here and abroad. Collectively, they may be estimated to cost our country each year as much as the cost of all the research that has been done throughout the world in this field since virus studies began.

It will probably continue to be true that conspicuous diseases like spotted wilt in tomato will attract attention to the losses involved wherever they occur, and that inconspicuous diseases will produce greater damage with less accompanying publicity. Because some viral diseases have not yet attained world-wide distribution, it would appear in the interests of national welfare that whatever agencies are prepared to do research on viral diseases should emphasize preparation of control measures before these are desperately needed. They should, of course, study the characteristics of, and prepare control measures for, inconspicuous but costly, as well as obvious and well publicized, viral diseases.

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ORIGIN AND DISTRIBUTION OF NEW OR LITTLE KNOWN VIRUS DISEASES

C. W. Bennett

It is a significant fact that well into the present century recognized crop losses due to virus diseases were relatively minor when contrasted with those caused by other agencies. Even as late as 1920 few scientists would have predicted the marked increase in economic importance of virus diseases that has taken place during the past three decades. With the exception of sporadic outbreaks of a few diseases such as peach yellows in northwestern United States, widespread serious injury to crop plants as a result of virus attacks was almost unknown. In fact, even after the beginning of the more extensive study of virus diseases that started about 1920, the increased interest in this group of pathogenic agents was considered by some to be a passing fad which was attracting more attention than it merited and the opinion was voiced that many of the plant pathologists who had strayed into the field of virus research soon would return to the more important and profitable field of investigation of fungus and bacterial diseases. At that time probably few plant pathologists would have disagreed seriously with these conclusions.

However, instead of remaining static or increasing in importance in proportion to other types of plant diseases, damage due to viruses has increased enormously in recent years in many of the agricultural areas of the world. During the past 30 years more than 200 virus diseases on a wide range of host plants have been described as new. Many of these are now of major concern. A few examples may serve to illustrate the importance that some of these diseases have assumed in crop production.

Tristeza of citrus has destroyed seven million orange trees in the State of São Paulo, Brazil, alone, and has attacked or now threatens many other millions of trees in tropical and subtropical areas throughout the world.

Swollen shoot of cacao has decimated the cacao industry in parts of west Africa and constitutes a serious menace to the entire cacao industry.

Peach mosaic has caused the destruction of thousands of peach trees in western United States, and sugar beet yellow wilt has destroyed a sugar beet industry in the Rio Negro Valley of Argentina. It is worth noting that not one of these diseases was recognized prior to 1930.

The origins of these relatively new diseases and the reasons for the marked increase in their numbers and in the damage they produce pose questions of more than academic importance. It is possible, of course, and even probable, that some of these newly described viruses have existed undiscovered in economic plants for many years. This may be true of a number of viruses that produce relatively minor injuries. However, it is difficult to believe that the major portion of these 200 or more viruses have been perennial inhabitants of common crop plants. Moreover, many of them have histories of occurrence at first only in limited areas and apparent spread from points of origin.

On the basis of available evidence we are forced to the conclusion that many of these viruses have either originated de novo in recent years, or they have spread to crop plants from sources where their presence is not easily detected.

No evidence is available to show that new viruses are being initiated in plants under natural conditions, although it is known that some viruses do change to produce variants of the original forms. In some cases these variants may be more destructive than the parent virus but they can hardly account for a large part of the increased injury to crop plants.

It seems much more probable that most of the increase in the number of recognized viruses and in the injury they cause has resulted from the more widespread dissemination of viruses that have existed more or less as localized entities for many decades and perhaps for many centuries. This concept is supported by the records of origin and spread of many of the more recently discovered virus diseases. In this connection, it is significant that the majority of new viruses have been found in the newer agricultural regions of the world. For example, relatively more new viruses have been described in North America than in Europe; and recently, on certain host plants at least, more new viruses have been found in western than in eastern United States.

The sequence of appearance of new virus diseases on certain specific crop plants appears to throw further light on the question of origin of new viruses. Peach and sugar beet may be selected for purposes of illustrating acquisition of viruses by different species of plants as their culture has expanded into new geographical areas. Many other species, particularly grape, citrus, and tobacco have more or less similar histories of attack by new virus diseases.

When the peach began to be grown in eastern United States in the earlier years of expansion of agricultural enterprises in this region it was attacked by peach yellows, little peach, phony peach,

and rosette. These were all virus diseases new to peach and they still occur over a limited area, probably owing to limited distribution of their insect vectors. For a period of many years these were the only virus diseases known to occur on peach in the United States. However, as the growing of peach and other stone fruits expanded westward to the Pacific Coast, these species were attacked by other virus diseases. Beginning about 1930, new virus diseases of stone fruits appeared in rapid succession and in the succeeding 20 years many new virus diseases were found not only on peach but on other kinds of stone fruits that had hitherto been relatively free of this type of disease. A recent publication[1] lists and describes 48 virus diseases of stone fruits in the United States and Canada. About 38 of these have been discovered during the past 20 years.

It may be suggested that viruses are found where one looks for them and that the reason for discovery of this large number of new virus diseases on stone fruits lies in the fact that recently more pathologists and horticulturists have become interested in viruses of this group. However, tabulation of the place of presumed origin of these viruses reveals the fact that of the 38 virus diseases described during the last 20 years, 31 were found first in the Rocky Mountain region and west, and only 7 were found in the eastern part of the Continent. Since it may be assumed that pathologists and horticulturists of the two regions are equally alert to the appearance of new diseases, it must be assumed that more new virus diseases actually have attacked species of stone fruits in western than in eastern United States and Canada during this period. Even some of the new diseases found in the eastern section, such as peach ringspot and cherry yellows, are of a type that may have existed undiscovered in peach and cherry or related species for many years.

The history of acquisition of virus diseases by the sugar beet is of still further interest. Beta vulgaris, from which the modern sugar beet was largely derived, is thought to be a native of the eastern Mediterranean region. So far as known, it is not subject to attack by any virus disease in its original native habitat, but reliable evidence on this point is not available. Transported to central and northern Europe it was attacked by "kräuselkrankheit" in Germany and by mosaic and virus yellows over much of western Europe.

When the sugar beet was introduced into western United States and began to be grown extensively, it was attacked by another new and destructive virus disease -- curly top -- which resulted in the abandonment of the industry over extensive areas before resistant varieties were available for planting.

Introduced into the Rio Negro Valley of Argentina in 1929, sugar beet was attacked immediately by another new virus disease now known as yellow wilt. The Río Negro Valley has soil and climatic conditions admirably suited to sugar beet culture. Despite this fact, however, yellow wilt was so destructive that the highest average yield in any one year was about six tons per acre and in the worst seasons the crop was almost a total loss. The industry was abandoned ten years after it was initiated, after heavy loss to farmers and to the sugar company operating there.

One may conclude from these records of acquisition of virus diseases by stone fruits and sugar beet that these plants have picked up new virus diseases in each major area into which they have been introduced. In fact, it seems to be true generally that when a cultivated species begins to be grown extensively in an area new to its culture it is likely to be attacked by virus diseases to which it has not before been subjected. Some of these diseases, of course, may be known virus diseases of other crop plants of the area, but, in many instances, virus diseases of recently introduced crop plants have been caused by previously unknown viruses.

This type of evidence is now available for viruses of so many plant species in so many areas of the world that it seems virtually certain that each major geographical area is inhabited by viruses many of which had only a limited distribution before the era of modern agricultural expansion and development. The most logical original source of such viruses is native uncultivated plant species and, perhaps in some cases, cultivated species that have been associated with local viruses for so many years that they have acquired a high degree of resistance.

It seems probable that viruses have originated largely in uncultivated plants in past ages. How often new viruses have arisen and by what method, is wholly unknown. During the earlier periods of the development of an agriculture, new viruses probably had limited opportunities to spread because of the isolation of agricultural communities and limited transport of plant products. Under such conditions, and over long periods, cultivated as well as uncultivated species would be expected to acquire a high degree of resistance to local virus by natural selection. Thus a state of equilibrium between plant viruses and their hosts was maintained in which the host plants suffered only a minor degree of injury.

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[1]Virus diseases and other disorders with viruslike symptoms of stonefruits in North America. Agr. Handbook 10, U.S. Dept. Agr., 276 pp. 1951.

With the opening of vast areas to the production of new crops in recent years, the domestication of many new species, and the widespread dissemination of plant products that has come with modern methods of transportation, the balance between viruses and their host plants that was maintained for centuries has been upset drastically. Plant species resistant to viruses over their original areas of distribution have been transported to many other areas of the world, where they encountered viruses with which they had never before been associated and to which they had had no opportunity to acquire resistance. Many of these viruses, after they have been transferred from indigenous to newly introduced species, have been transported in various ways to many other areas as new virus diseases.

This process of release of viruses from resistant wild and cultivated species to new crop plants probably has been proceeding at an accelerated pace during recent years. We may only guess as to how much time will be required for viruses to attain their maximum distribution under present conditions.

No estimate of the number of potentially destructive viruses that remain hidden in the wild plants of various parts of the world may be made at the present time. However, it seems probable that many viruses still may be present undiscovered in uncultivated species, or even on some cultivated species, in various parts of the world and that many of these will find their way eventually to economic plants on which they will be able to cause serious losses.

Obviously, detection of viruses in wild plants and in resistant cultivated species in which they produce very minor symptoms, or none at all, is difficult. However, there is good reason to believe that such viruses exist and that some of them, at least, could be discovered by diligent effort. Actually, a few such viruses are known already. One in particular has been studied sufficiently to permit speculation as to its potentialities for production of damage to crop plants.

This virus was discovered by accident in 1937 when some sprigs of dodder, Cuscuta californica, were collected in southern California and placed on sugar beet plants in the greenhouse with the expectation that they would be used later in transmission tests with sugar-beet curly-top virus. Much to the surprise of those concerned, the sugar-beet plants infested with this dodder came down with a virus disease not before observed on sugar beet. It developed that this disease was caused by an undescribed virus that proved to be able to attack not only sugar beet but tobacco, potato, tomato, celery, pokeweed, and cantaloupe. It was particularly severe on cantaloupe. Field-inoculated cantaloupe plants produced runners less than a yard long and the melons were small and of inferior quality.

In this virus we have an apparently native disease-producing agent that discloses no indication of its presence on wild host plants, so far as known. Nevertheless, it is able to attack a number of crop plants and it may hold potentialities for causing heavy losses, particularly to the cantaloupe and muskmelon industries of the Coachella and Imperial Valleys of California, and perhaps other areas. All that is now required for this virus to become a destructive, disease-producing agent is the intervention of a vector that can transfer it from the native hosts and spread it extensively on crop plants. If this should occur, we might well have an outbreak of a destructive new virus disease.

Certain other viruses that have only recently escaped from native host plants constitute an even more definite threat to cultivated plants. One which is particularly menacing is yellow-wilt virus of sugar beet. Since the destruction of the sugar-beet industry in Argentina by this virus it probably again is more or less limited to its original host plants. This virus apparently is disseminated by a leafhopper, Atanus exitiosus, that has a limited distribution at present. The area of its known occurrence, however, has climatic conditions similar to those of Idaho and Utah. Therefore, there is reason to fear that it would thrive over a large part of the sugar-beet producing area of western United States. If this leaf-hopper should be introduced with the virus which it presumably transmits, sugar beet production would become unprofitable in all areas of the United States in which the disease proved to be as destructive as it was in Argentina.

With the continued expansion of the culture of various species of economic plants into all areas of the world where they will produce profitable yields, and with the modern methods of rapid transport of plant products in large quantities, it may be expected that, sooner or later, most virus diseases will achieve a maximum distribution determined by their host and vector relationships. Quarantine measures may be expected to delay this spread, perhaps in some cases for many years, but they can hardly be expected to prevent it.

It seems probable that agricultural production has entered a period in world history that is requiring, and will continue to require for many years to come, drastic modification of species and varieties of crop plants to counteract damage by viruses able to attack them. Control of virus diseases, already a very important phase of agricultural production, is likely to demand increased effort for an appreciable period in the future. Since, as a rule, virus diseases are not

so readily controlled by use of the conventional methods employed to combat fungus and bacterial diseases such as application of sprays, sanitation, etc., it seems probable that in the long run discovery or development of resistant varieties will need to be relied on to a very large degree for solution of many of the production problems posed by the increase in numbers and destructiveness of virus diseases. This may involve replacing many of the varieties now grown with varieties that have a greater degree of resistance to certain virus diseases. It may even involve the temporary abandonment of the growing of certain crops in some areas and their replacement by others more resistant to viruses.

In fact, in some areas, the impact of certain virus diseases on agricultural crops has already played a major part in bringing about important changes in the varieties of certain important crop plants that can be produced profitably. For example, in the past 30 years it has been necessary to replace nearly all of the varieties of sugar cane formerly grown in the Western Hemisphere with varieties resistant to sugar cane mosaic, and all of the varieties of sugar beet grown in western United States have been replaced since 1932 by varieties resistant to curly top. Also, the tristeza disease of citrus is forcing major changes in the citrus industry in much of the citrus-producing area of the world and its presence probably will result in virtual elimination of the sour orange as a root stock. This will be a major loss in a number of citrus-producing areas because of the resistance of this species to root rots.

It seems certain that virus diseases will continue to be important factors in crop yields for many years. The extent of losses to be expected will depend in part on the number and nature of new virus diseases that appear, and in part on the success of control measures. In any event, it seems probable that, for many years to come, the problem of reducing losses from virus diseases will constitute a distinct challenge to the industry and ingenuity of farmers, plant pathologists, geneticists, entomologists and many others concerned with improving yield of crop plants.

DIVISION OF SUGAR PLANT INVESTIGATIONS, BUREAU OF PLANT INDUSTRY, SOILS, AND AGRICULTURAL ENGINEERING, AGRICULTURAL RESEARCH ADMINISTRATION, UNITED STATES DEPARTMENT OF AGRICULTURE

THE ROLE OF INSECT SURVEYS IN VIRUS-VECTOR RESEARCH

William F. Turner

Virology is a very young science. The detection and study of vectors are of even more recent inception. So I think we may point with pride to the number of vectors that have been discovered and to the considerable body of knowledge that has been built up concerning them. Nevertheless, we must recognize that for a great number of viruses, many of them of primary economic importance, no vectors have yet been discovered. This situation not only offers a challenge to the investigator, but also constitutes a serious hindrance to further studies of the viruses themselves and particularly to control of the diseases caused by them.

A sufficiently large number of vectors have been discovered to permit us to achieve a certain amount of classification. We may presume that the vector will be an insect with sucking mouth parts -- probably a homopteron. If the virus causes a mosaic disease, we should expect the vector to be an aphid; if the disease is of the yellows type, we should look for a vector among the Cicadellidae, or possibly the Fulgoridae or Cercopidae. However, the classification of viruses is still in a fluid state and our total number of known virus-vector associations is still so small that we are not justified in making firm pronouncements, even as to the probable family to which a vector belongs.

When we narrow the field to a search for single species, the identity of an unknown vector may be even less obvious. Of course, in order to transmit a disease, the insect must feed on the plant involved, but there is no certainty, nor even a probability, that the vector will prove to be an insect having specific relationships with the plant in question. In fact, the relationship may range from an obligatory one to one involving merely casual visits. Macropsis trimaculata (Fitch) breeds only on plants that are subject to attack by the virus it transmits. Myzus persicae (Sulz), which spreads many different diseases, is a very general feeder and may be a primary or only a secondary pest on the host to which it is transmitting a virus. Draeculacephala minerva Ball and Carneocephala fulgida Nottingham are important agents in the spread of Pierce's disease, yet grapes are not the normal hosts of these insects.

Thus, while some vectors are almost obvious, many are "the last insect one would suspect." Were this not so, we should expect to know the vectors of far more viroses than we do, and it is this very obscurity that presents the greatest challenge to an entomologist and calls for the exercise of all his ingenuity in devising modes of attacking the problem.

Surveys have always been used in some measure as an aid to vector detection, even though limited to a collection of insects from a single group of diseased plants, or perhaps conducted at second-hand through a compilation of records derived from a study of the literature. However, reports of the discovery of vectors rarely furnish detailed information as to the methods employed in selecting suspects, and the extent of the survey activities involved can seldom be determined, even by inference. Because of this situation any exposition of the survey method of approach must be largely based on first-hand information with reference to studies on one disease.

Insofar as we know, the first vector-research program based on a detailed survey was formulated by L. D. Christenson as a mode for discovering the vector of phony peach. At the time the Bureau of Entomology and Plant Quarantine undertook this program, the virus was known to be present in the roots of affected trees, but all attempts to transmit the disease by budding or by grafting with scions had failed. Thus, it appeared probable that the virus was confined to the roots of the trees and that the vector must be a root-feeding insect. From such knowledge as we then had concerning soil fauna, the only groups that came readily to mind as in any way meeting the requirements were root aphids, Cydnidae, nematodes, and possibly mites, though there were reasons for doubting the ability of any of these groups to transmit this particular disease. Obviously, the first thing to do was to determine just what insects occur in the soil of peach orchards.

Phony peach attacks trees growing in a great diversity of soil types, from sand to heavy clay and from acid to strongly alkaline. It was certain that the fauna would vary markedly in these soils and that collections would have to be made from as many different types as possible. The disease appeared to have become fairly stabilized in general distribution. Local spread was rapid in the Gulf States, but the rate decreased in intensity to the north and west until a point was reached where local spread no longer seemed to occur. Presumably, this decrease in the activity of the disease was due to a similar decrease in the prevalence of the vectors, and perhaps to their entire absence beyond the periphery of the area in which any spread occurred. It therefore seemed reasonable to make collections not only in orchards in which the disease was of serious importance, but also in others where the incidence of spread was low, and finally in orchards in which the dis-

ease had been introduced but had failed to spread. As eventually developed, the project called for a survey of soil insects in peach orchards scattered from Georgia to Texas, and north as far as Illinois, Kentucky, and Maryland.

At first, survey activities were confined to soil collections, but shortly after our work began the pathologists developed information leading them to suspect that the virus might sometimes occur in the tops of affected trees, and they suggested that we give serious consideration to this possibility in conducting our survey. Consequently, the work was expanded to include collections from aerial portions of the trees. Further study suggested the advisability of considering an "orchard" as not being restricted to a group of trees, but as including all the flora occupying a given area and dominated by a group of peach trees. So once again we expanded our operations to include collections from all ground cover in the orchards.

The survey was necessarily exploratory in the beginning, but after a few weeks we settled down to approximately 30 primary collecting stations. Ideally, each station was to be visited at intervals of two months, but in practice we found that it was not feasible to visit them oftener than about four times a year. From time to time we made collections in additional orchards, a total of 112 stations receiving one or more visits.

All insects, in fact all creatures collected from the soil, were preserved, as were all Homoptera, Hemiptera, Thysanoptera, and mites taken on the trees or on ground cover. Records were made of (1) the types of soil encountered, (2) the cultural state of the orchards, (3) their surroundings, and (4) the species of plants growing in them. We found that the second and fourth of these factors were of primary importance to the advancement of our project; nevertheless, the other two furnished desirable information and we should include them in any future survey.

After several months we made a careful analysis of the data obtained from the soil collections. This study failed to indicate any insects that offered promise as suspects. Similar studies of collections from the aerial portions of the trees brought to light only three species of Cicadellidae that were definitely associated with peach, all three being leaf feeders. No aphids were common on peach in the area where phony disease was prevalent.

Meanwhile, advancements in knowledge of the disease itself had led the pathologists to conclude that the virus did occur in the tops of phony-affected trees, but that it was confined to the xylem. These findings brought about a complete reversal of emphasis in our operations and the first step in narrowing our field. Top-feeding insects, which had previously received only secondary attention, now became the primary object of our search. Moreover, it appeared certain that the vector was a stem feeder, probably a leafhopper, that occurred on peach only occasionally or perhaps seasonally, but was generally present in orchards where spread of the disease was rapid.

We collected a total of 530 species of Homoptera, of which 382 species belonged to the Cicadellidae.[1] Analysis of our records on the basis of geography, host, and habits resulted in the compilation of a tentative list of 30 species of Homoptera as suspects. Data furnished by intensive surveys in orchards with records of high incidence of spread led to a further refinement of our list to four primary suspects, with some six other species doubtfully possible. These four primary suspects were all sharpshooters (Tettigellinae): Homalodisca triquetra (F.), Oncometopia undata (F.), Cuerna costalis (F.), and Graphocephala versuta (Say). All four of them proved able to transmit phony disease under experimental conditions. Thus, vectors of this disease were detected, without preconceived opinions, through the application of cold logic to data derived from surveys. The process proved to be a very satisfying one. We were confident that we had discovered vectors two years before we were able to secure experimental proof.

A feature of the disease itself that emphasized the success of this method was its long incubation period of two or more years in the plant. Had the incubation period been one of weeks instead of years, certain species of insects might have been tested on the basis of hunches, and the vector might or might not have been found before the survey was completed. As it was, the survey had produced highly probable suspects long before success might have been anticipated from hit-or-miss transmission tests. Actually there was little hope for an inspirational selection of vectors, because none of the four species has ever been considered a "peach insect."

Such a complete survey might not be justified as a method for detecting all vectors. It is quite true that with some vectors -- perhaps more commonly with aphids -- the suspects are less obscure than they were for phony peach. However, we feel that portions of the method, if not the complete program, will be called for in searches for many of the vectors that are now unknown. As we said earlier, were the identity of such vectors at all obvious, they would not be "unknowns."

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[1] Approximately 22,000 lots of insects were secured, each lot being a collection of one species. This material was examined and identified for us by the Division of Insect Identification -- a major task!

The discovery of a vector is certainly of primary service in advancing investigations on viroses, and perhaps is the most laudable contribution that entomologists can make to virology. However, such a discovery is only a start on the real objective, which is the preservation of a crop needed by man or at least the achievement of conditions that will permit man to produce the crop profitably. This may be accomplished by preventing spread and by direct control in areas where the disease already occurs. Logical measures designed to achieve either purpose must be based in part on a knowledge of the identity of the vector and, equally, of its way of life. This entails a further use of survey methods, though of a type differing somewhat from those followed in the preliminary research.

Prevention of spread almost inevitably involves the use of quarantines. Without knowledge regarding the habits of the vector, such quarantine features as width of an adequate barrier zone or the season during which movement of the plants is permissible can be determined only arbitrarily as a compromise between guesses. Logical standards are necessarily based on information concerning the flight habits of the vector, its seasonal association with the plant or crop, and the degree of risk attendant upon its attraction or lack of attraction to young plants. All these factors can be determined only by intensive field surveys.

Similar information is needed for the development of control measures. At present, inspection and roguing are the only known methods for attacking many virus diseases. Admittedly these are merely palliative measures, serving to check rapidity of spread but only occasionally procuring actual reduction or local eradication of a disease. Isolation of plantings is receiving more and more attention, and this may well be the answer to the virus problem with certain row-crop diseases. It presents less hope for the orchardist, who must maintain his plantings for years in the same location, where they are often exposed to neighboring wood lots, border plantings, and fields over which he has no control. Other measures under investigation include timely planting, breeding of immune or resistant varieties, and the use of insecticides against the vectors. Some of these appear promising, within definite limits, but for the present we must still depend on roguing if we are to prevent a number of viroses from getting out of hand.

It has been necessary to initiate most control projects without the benefit of knowledge concerning vectors. Once the identity of such vectors is known, it appears probable that studies of the behavior and habits of these insects will yield information that will materially increase the efficiency of the roguing method of control. An an example we may consider seasonal association between the vector and the host plant. Vectors may feed on a host during spring, summer, or fall or, as is the case with the principal vectors of phony peach, during both spring and fall. Obviously, knowledge of such seasonal association is an important guide to the proper scheduling of roguing operations. If trees are cut or removed during a period when the vectors are feeding on them, the insects are inevitably driven to other trees, and the activity designed to control the disease actually may contribute to its dissemination.

Information concerning vector distribution may be of fundamental importance in planning geographical emphasis in a control program. By this we do not mean simply that no control effort is needed beyond the distributional limits of the vector. The situation may be much more complicated than that. Four species of Cicadellidae are able to transmit the phony peach disease. It has been demonstrated that two of them, H. triquetra and O. undata, are natural vectors; the role of the other two is still in doubt. H. triquetra is a strictly southern species, while O. undata ranges much farther north. A comparison of the rate of spread of the disease as recorded in the course of large-scale control operations with our survey records on distribution of the insects furnishes strongly presumptive evidence that H. triquetra is the most important vector. These studies indicate that O. undata can maintain a slow spread of the disease, but the incidence becomes serious only when H. triquetra is also present. It is obvious that the control project needs to be informed not only about the distribution of the vectors as a group, but also on the distribution of at least one individual species. As an example of the usefulness of such information, should it become necessary to make a choice of regions in which work could be performed during any one year because of curtailed funds or insufficient personnel, areas where O. undata only is present could be disregarded temporarily without fear that the disease would build up to a dangerous level.

Among other menas of control being practiced or investigated in the case of some virus diseases are cultural methods and chemical control of the vectors. Cultural methods may deal directly with the handling of annual crops or with such practices as interplanting or clean cultivation of perennial crops. Studies have already indicated that timely planting in relation to insect activity may be a very important factor in decreasing the initial infection and subsequent rate of spread of viroses attacking some row crops. Investigations of insect behavier leading to these effective practices have been based on surveys, often covering large areas and extending far outside the region where the affected crop is grown. An outstanding example of this type of operation is the series of ex-

tensive surveys that have been made of the seasonal range and feeding habits of Circulifer tenellus (Baker), the vector of curly top.

For perennial crops other cultural practices may be very important factors with relation to attack by virus diseases. Some viruses have a wide range of plant hosts, and the vectors of some viruses are very general feeders. In locating a new orchard or vineyard it is important that thought be given to the surroundings, particularly to the juxtaposition of wild hosts of a virus itself or of its vectors. Later, the type of vegetation grown as an intercrop, or allowed to grow as a covercrop, may largely determine the course of a virosis in an orchard or vineyard. In this connection, the importance of the survey method has been demonstrated by investigators working on Pierce's disease. Their surveys extended far outside the area where grapes are grown. Collections were not confined to those insects known to transmit the disease to grapes but included all species of Tettigellinae. The data furnished by these studies demonstrated that the virus has a wide range of hosts among wild perennials, that it is of widespread distribution in wild hosts, and that several species of insects that never attack grapes play an important role in the dissemination of the disease because they maintain a reservoir of inoculum in wild host plants.

Chemical control of vectors as a mode of combating virus diseases is still in an experimental stage. Although benefits seem to have followed use of sprays in a few cases, most investigators have reported merely encouraging results or failures. Certainly, any success from the application of insecticides must depend on operations based on knowledge of the life history of the insect and also on its behavior.

Some aphids breed on a host throughout the growing season, or at least for a definite period, without any marked tendency to make major migrations into or out of a field. Such aphids appear amenable to control with a fairly simple schedule of spray applications. On the other hand, some aphids have only a transitory association with a particular crop as individuals, but because they are of a restless nature the crop is subject to frequent or almost continual invasion from without. Moreover, in many of these vectors the latent period is extremely short or non-existent, so that transmission can be accomplished in a matter of minutes. In such crops there appears to be little hope of obtaining any satisfactory control of the disease with insecticides.

Against some leafhopper-transmitted diseases we have reason to hope for successful results by spraying. In one instance growers seem to have achieved a large measure of control without deliberately attempting to do so. Certainly, in commercial orchards peach yellows has decreased in importance in late years, although it still spreads rapidly at times in home orchards and in escapes. It has been suggested that this may be due to a marked reduction of the vector population through the use of sprays containing wettable sulfur, although there appears to be no experimental evidence to support the hypothesis. Since Macropsis trimaculata lays its eggs in twigs of peach trees, heavy pruning may have contributed to the reduction through the removal and destruction of these eggs. In any case, the insect should be easy to control, since it does breed on peach trees and has only one generation per year, with active stages lasting from late in May to early in August. A single application of DDT about the middle of June should be sufficient.

For other leafhopper-borne viroses, the control of the vectors is not so simple, but there appears reason to hope that benefit may be achieved in some cases, especially when the association of the vectors with the host is definitely seasonal rather than sporadic. Spraying alone may never produce enough control of the insects to have a material effect on the course of the disease, but spraying combined with roguing might establish a descending rate of spread that would eventually reduce the disease to an innocuous state.

The propriety of even attempting such measures of control must be determined through knowledge of the relationship existing between the vector, or vectors, and the host plant. Is direct association periodic or sporadic? Do the inseots remain in the orchard while feeding on other hosts, or do they usually invade it from distant points? Is the situation complicated by the cultural practices followed and by the types of crops being grown outside the orchard but adjacent to it? What are the over-wintering habits of the vector? Is the insect susceptible to attack on other host plants? Obviously, there is only one method by which such questions may be answered.

Virus diseases of plants, although of recent recognition, are becoming increasingly important not only as fascinating subjects for investigation, but also as threats to National and world economy. There can be no doubt that the detection of vectors of these diseases and the discovery of methods for controlling them constitute a major contribution to the fight against the diseases themselves. In such studies surveys appear to offer an important method of approach.

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INSECT VECTOR-PLANT VIRUS RELATIONSHIPS

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Leafhoppers were the first group of insects shown to be capable of transmitting plant viruses, according to Fukushi (9). They are responsible for the dissemination of a number of economically important plant viruses including some of the stone fruit viruses. Aphids are the most important known insect vectors of plant viruses and they transmit more viruses than any other group of insects. Among other suctorial insects whiteflies, mealybugs, tingids, cercopids, and fulgorids are the vectors of a limited number of viruses. Thrips are known to transmit only one plant virus, tomato spotted wilt, which has a world-wide distribution. Insects with biting mouthparts such as beetles and grasshoppers are responsible for the transmission of a few viruses. It will not be possible to discuss all the insect vector-plant virus relationships in this report because of the great mass of details. An attempt will be made to deal with the general relationships of plant viruses to aphids, leafhoppers and mandibulate insects. These relations are repeated in the other smaller groups of vectors with specific variations.

Early workers believed that insect-transmitted plant viruses could be divided into two groups, those thought to be transmitted mechanically by contamination of mouthparts such as the majority of the aphid-borne viruses, and those involving a more complex biological relationship such as the leafhopper-borne viruses. The evidence for the contamination of mouthparts hypothesis consisted of the ability of aphids to transmit the mosaic viruses immediately after feeding only a few minutes on a diseased plant, and their ability to retain the capacity to infect plants for only brief periods of time. It was assumed that the insect was acting merely as an inoculating needle in the transmission of the virus. As opposed to this, the biological transmission hypothesis was supported by the fact that this group of viruses required a latent period in the insect vectors before they became capable of infecting healthy plants and once the insect was infective it retained the capacity to infect healthy plants for long periods of time.

While basically this generalized grouping still persists, the more recent work indicates that the earlier assumptions are not as simply explained as was at first believed, and somewhat different interpretations are given the observed phenomena. The evidence now indicates that while there are many insect vector-plant virus relationships which appear to fall naturally into two groups, others have variable characteristics the significance of which is not understood.

Watson and Roberts (23) have suggested the terms persistent and non-persistent to better designate the two types. The non-persistent viruses are usually aphid-borne and are characterized as follows: (a) they are usually readily transmissible by mechanical inoculation; (b) increased efficiency results from starvation of aphids prior to short acquisition feeding periods; (c) aphids retain this type virus for only short periods of time; and (d) there is a general lack of specificity of the aphid vectors. The persistent viruses are typically leafhopper-borne, although a few are transmitted by aphids, thrips, and whiteflies, and they are characterized as follows: (a) they are not usually transmissible by mechanical inoculation; (b) evidence indicates the necessity of the latent period in some cases before they can transmit; (c) they retain this type virus for long periods of time, often for the life of the insect; and (d) there is a greater degree of specificity of vectors.

Mechanical transmission of plant virus was rejected by Watson and Roberts (24) who demonstrated that starving aphids, preceding a short feeding on a diseased plant, greatly increased the efficiency of virus transmission. If the feeding period on the diseased plant was increased to an hour, the beneficial effect of the starvation was lost. These results do not support the hypothesis that the aphids transmit the virus by mere external mechanical contamination of mouthparts, since there is no reason why a starved aphid should have its mouthpart more heavily contaminated than an unstarved aphid, nor why an aphid fed for a short period on a virus source would be more efficient than one fed for long periods. The results indicate a lack of mechanical transmission, and the presence of an inactivator which does not operate if the aphids are starved and fed only briefly.

The extremely short periods of time necessary for the aphid vectors of some viruses to effect the transmission from a diseased to a healthy plant are difficult to interpret. Sylvester (21) has transmitted the sugar-beet mosaic virus by the green peach aphid from a diseased plant to a healthy plant in as short a period as 42 seconds. The short feeding times involved seem to preclude the possibility of the virus being taken up into the body of the aphid and returned to the plant. These results suggest that the virus is merely taken up into the mouthparts and immediately returned to the plant. Two suggested explanations are, first, a small amount of infective sap taken in the food canal of the aphid's proboscis during the feeding on a diseased plant might be released when the aphid begins to feed on a healthy plant, or, second, there might be a short circuit by a

leakage between the food canal and the salivary canals resulting in an outward flow of infective sap with the salivary secretion resulting in infection.

The non-persistent aphid-borne viruses are retained by their vectors for only short periods of time. The aphids usually infect only the first plant on which they feed following an acquisition feeding on a diseased plant. If the time the aphid is allowed to feed on each of a series of plants is reduced to a few seconds, a single aphid may infect a number of plants either consecutively or at irregular intervals. These results, showing that an individual aphid is capable of infecting a number of plants when transferred from a diseased to a series of healthy plants, are not logically explained by assuming external contamination of mouthparts.

In general there is only a low degree of specificity among the aphid vectors of plant viruses, e. g. the onion yellow dwarf virus has been transmitted by some 50 different species of aphids (6) and 17 species of aphids have been shown to be vectors of western celery mosaic virus (18). However, not all species of aphids will transmit a given virus. Although the green peach aphid has been reported to transmit more than 50 different viruses there are certain viruses such as the dandelion yellow mosaic virus which the green peach aphid has failed to transmit, but which is readily transmitted by other aphid species (12).

Aphid species vary significantly in their efficiency in transmitting plant viruses. While a large number of viruses are most efficiently transmitted by the green peach aphid, some viruses are more efficiently transmitted by other species. The eleven species of aphids tested for ability to transmit western celery mosaic (18) varied in their efficiency from 92.5 percent infection by the rusty-banded aphid Aphis ferrugineastriata Essig, to only 2.2 percent by the dock aphid, Aphis rumicis Linn.

When dealing with the leafhopper-borne viruses of the persistent type we are seemingly faced with a more intimate vector-virus relationship -- a biological one. The evidence for a biological relationship and for multiplication of plant viruses in the body of leafhopper vectors has been greatly strengthened by recent experimental results. Originally the latent period and the long retention of the virus by the leafhopper vector were the main evidence for multiplication.

Two leafhopper viruses have now been demonstrated to be transmitted through the egg of their vectors. The rice stunt virus has been shown by Fukushi (10) to be transmitted through the egg of the leafhopper Nephotettix apicalis (Motsch.) for seven generations. Over 1,000 infections were produced by the offspring derived from a single virus-infected egg. The clover club-leaf virus has been maintained for five years through 21 generations of the leafhopper vector Agalliopsis novella (Say). Black (3) estimated the minimum dilution of the virus in the insect to exceed 2.8×10^{-26} if no multiplication is assumed. The only logical conclusions that can be derived from such results is that the virus must have multiplied within the body of the insect vector.

Leafhopper to leafhopper transmission of plant viruses by needle inoculation was first demonstrated by Storey (20). This technique was used to good advantage in demonstrating that plant viruses multiply within the body of their insect vectors. Black (2) succeeded in transmitting the aster yellows virus at low temperatures from virus-carrying aster leafhoppers to noninfective leafhoppers by means of fine glass capillaries. His results indicated that there was more virus in the body of the insect vector 12 days following a one-day acquisition feeding than at 2, 4, or 8 days.

Serial passage of aster yellows virus from infective to noninfective leafhoppers had been accomplished by Maramorosch (16). He reports no decrease in virus concentration in the insect after eight serial passages. The wound tumor virus has also been serially transmitted through its leafhopper vector by Black and Brakke, according to Maramorosch (15). These results provide further substantial evidence for multiplication of these viruses within the body of their insect vectors.

Maramorosch (14) showed that the latent period in the leafhopper vector of aster yellows virus was longer in insects infected with diluted virus and shorter in insects receiving more concentrated virus. The results suggest that the multiplication of a small amount of virus takes a longer time to render the insects infective than a larger dosage.

The site of the virus multiplication in leafhoppers has not been indicated and few suggestions have been offered as to its location. The virus has been demonstrated to occur in the blood, salivary glands, and the alimentary tract. The amount of virus present in the salivary glands has proved to be low and the results suggest the blood as the main reservoir of virus.

The transmission of curly top virus by the beet leafhopper Circulifer tenellus (Baker) appears to differ fundamentally from the transmission of such viruses as aster yellows, rice stunt, clover club leaf and wound tumor virus. The evidence reported by Freitag (7) and Bennett and Wallace (1) seems to indicate a lack of multiplication of the curly top virus in the vector. The charge of virus carried by the leafhopper varies with the length of feeding time on diseased curly top beets.

Insects fed for short periods on a virus source acquire only a light charge of virus and infect only a small number of plants when transferred daily to healthy plants. Those fed for long periods on a curly top plant acquire a heavy charge of virus and infect a number of plants, but even these insects gradually lose their virus charge and lose the capacity to produce infection. Leafhoppers which have lost their virus charge can replenish it by feeding on curly top beets and can be demonstrated to have renewed their capacity to infect plants. If the curly top virus multiplied within the body of the leafhopper one could assume that once an insect acquired a charge of virus, no matter how light, it would be maintained by multiplication and the vector would not lose the capacity to produce infection nor need to restock its supply of virus. The most logical interpretation of the experimental results obtained is that the leafhopper acquires a certain charge of virus which is determined by the length of feeding time on a diseased plant, and that during the process of feeding the virus is gradually dissipated until the supply is exhausted and the insect becomes incapable of infecting healthy plants. If permanence of infective power during the life of the insect is a basis for the assumption that a multiplication of the virus occurs in the vector, it cannot be argued that a multiplication of the curly top virus occurs in the beet leafhopper.

Although the great majority of plant viruses are transmitted by insects with sucking mouthparts, others are spread by insects with chewing mouthparts. Doolittle (5) reported that cucumber mosaic was transmitted by the twelve-spotted and the striped cucumber beetles. Smith (19) transmitted the cowpea mosaic virus by means of the bean leaf beetle Ceratoma trifurcata Forst. and suggested the method of transmission. He showed that juice of abdominal contents regurgitated by the beetles fed on diseased plants was infectious when inoculated into healthy plants. Goss (11) showed grasshoppers to be vectors of potato spindle tuber virus. Larson and Walker (13) reported that larvae of Pieris rapae Linn. could transmit cabbage mosaic virus. The differential grasshopper Melanoplus differentialis (Thos.) is reported by Walters (22) to be the vector of tobacco mosaic, potato X virus, and tobacco ringspot. The insect vector of these three viruses has been an enigma for a number of years.

The results of investigations of beetle transmission of squash mosaic by Freitag (8), yellow turnip mosaic by Markham and Smith (17), and cowpea mosaic by Dale (4) have expanded our knowledge of the relationship between chewing insects and the transmission of plant viruses.

Dale (4) showed that the leaf beetle Ceratoma ruficornis (Oliv.) is an efficient vector of cowpea mosaic. He found that single beetles could acquire the virus in only three minutes feeding on a diseased plant and could immediately infect healthy plants during a similar period. Beetles fed for several hours on infected plants and then transferred daily to healthy cowpeas were infective for six days. Yellow turnip mosaic has been shown to be transmissible by three groups of mandibulate insects, beetles, grasshoppers and earwigs by Markham and Smith (17). Insects with sucking mouthparts such as the green peach aphid and some plant bugs were found incapable of transmitting the virus. Feeding periods of one to ten minutes proved long enough for mustard beetles to acquire the virus. The beetles retained the virus for a period of four days and the results suggested that the length of feeding period governs the number of plants subsequently infected. The beetles apparently do not become infective immediately, but a period of 24 hours must elapse following the infection feeding. Since beetles are generally not known to have salivary glands the results are best explained by transmission through regurgitation. The beetles are reported to regurgitate part of the contents of the foregut to aid digestion of leaf tissue and it seems logical that infection might take place during this regurgitation process.

Transmission of squash mosaic virus by the western striped cucumber beetle, Acalymma trivittata Mannerheim, and the western twelve spotted cucumber beetle, Diabrotica unidecimpunctata unidecimpunctata Mannerheim, was demonstrated by Freitag (8). The squash mosaic virus has been shown to be retained by the beetles for a period of 20 days. In view of these results simple mechanical transmission of squash mosaic virus would appear unlikely. A more plausible explanation of observed results would be by regurgitation as suggested by Markham and Smith (17). Another possible means of transmission might be through fecal contamination.

For example, an experiment was undertaken to determine whether the beetles might give off squash mosaic either through regurgitation or defecation. Twenty-five beetles were transferred from squash plants infected with squash mosaic to a sterile test tube for one hour, after which they were removed. The test tube was then washed with distilled water by shaking thoroughly for several minutes and the wash water was then inoculated into healthy squash plants. The wash was highly infectious and all plants inoculated developed symptoms. If the beetles were kept for several days on healthy plants preceding the time they were confined to a test tube, the wash was less infectious. However, the wash was still infectious following a seven day feeding on healthy plants, but it was not infectious after 15 days.

Squash mosaic virus was readily recovered from the macerated bodies of infective western striped cucumber beetles taken from diseased squash plants. The virus was also recovered from the bodies of beetles following a five day feeding period on healthy squash plants, but no infections resulted when beetles were fed twelve days on healthy plants. Blood obtained from infective beetles through the removal of hind legs or through shallow abdominal incisions proved to be infectious when inoculated into healthy squash plants.

SUMMARY

The methods of transmission of plant viruses by insects are not easily explained and there are a variety of relationships which are somewhat complex and difficult to interpret. The dissemination of viruses by aphids is not through simple external contamination. There is considerable evidence against such a relationship in the increased efficiency resulting from starvation, the significant variation in the ability of aphids to transmit different viruses, and the capacity of aphids to infect a number of plants when fed only briefly.

The transmission of two leafhopper viruses through the egg of their vectors and the serial passage from insect to insect of two other viruses, is strong evidence for multiplication and a biological relationship. Other leafhopper viruses such as curly top do not appear to multiply in their vectors.

The relationship between mandibulate insects and plant viruses is also not one of simple contamination of mouthparts, but appears to involve the process of regurgitation.

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